II. *On the Life History of* Drilus flavescens, Rossi.

By Lionel R. Crawshay, M.A. Oxon. Communicated by Charles Owen Waterhouse, F.E.S.

[Read November 5th, 1902.]

Plates I and II.

The following notes on *Drilus flavescens* are collected from observations made during the past three years. In July 1900 I first found the larva on the Downs, near Seaford, Sussex, and in this year reared five larvæ (all females), four of them emerging in the following spring, and the fifth continuing its growth for another summer. In 1901 I collected several more larvæ from the same locality, and from these I obtained in the spring of the present year (1902) a single male, and a few females, the remainder reappearing as larvæ.

In spots where snails—*Helicella itala* and *Helicella virgata* especially—cover the ground in immense numbers, it is not surprising that the larva thrives on its food-supply, and it may often be seen during the summer months, running hastily over the ground in search of food. Before passing to its life history, the form of the larva deserves some notice.

The larva, which is narrowed in front and much widened behind, has the upper surface of the abdomen rather thickly covered with coarse hairs of a bright burnt-sienna colour, springing chiefly from four longitudinal rows of fleshy processes, the processes increasing in length towards the posterior. The head is reddish-brown, flat above, with strong sharp mandibles, curving upwards and crossing one another above the labrum; the eyes consist of a single ocellus on either side. The antennæ (Plate I, fig. 1; Plate II, fig. 1) are two-jointed with a supplement to the second joint, and can be partially extended or withdrawn by the larva by means of a collapsible membranous tube which carries the first joint, the latter being thrust forward or partially withdrawn within the tube by a muscle which passes up the centre of it to the apex of the first joint. The second joint is somewhat flattened and bears at its

apex—on the inner margin a two-jointed supplementary process terminated by a long seta, and on the outer margin a smaller colourless process. The thoracic segments have a reddish-brown corneous covering above—marked with dark patches—with a few hairs. On each of the abdominal segments to the penultimate one the soft white body of the larva is protected above by a dark brown dorsal shield, sparsely hairy, bearing a bristly process on each margin, and by a pair of similar processes outside these, arising from the sides. The last segment has a single pair of larger bristly processes extending behind, with a spine at the apex of each, completing a covering which doubtless goes far to protect the larva from attack during its occupation of the snail-shell. The spiracles (Plate I, fig. 2) lie in an uncovered space between the dorsal shields and lateral processes, and project from small horny encasements which lie along the surface of the segments. A fleshy nipple on the under-side of the last segment aids the progression of the larva, and enables it to cling firmly to the surface of the snail-shell. It moves rapidly about the outside of the shell, aided also by a pair of small colourless pulvilli, attached by slender stalks to the base of the tarsal claw (Plate I, fig. 3).

The young larva, which is hatched about the middle of July, feeds till September, and then hibernates in the shell it has last occupied, attaining only a small size in the first year. This shell is evacuated in the following spring, and after this the larva may continue feeding at regular intervals till September. But owing to the existence of a distinct, inactive form for hibernation, and the fact that this may be assumed at any time of the summer, it is equally liable to pass nearly the whole of the year in a dormant state in the shell. Doubtless the larva often becomes full-fed in the year after hatching, but it probably more often feeds for a third summer. The full-fed larva then changes into a second hibernating form, pupating in the following spring, shortly before the appearance of the imago in May or June of the third or fourth year, as the case may be.

The snails which chiefly constitute its food in the locality referred to are *Helicella itala*, Linné; *Helicella virgata*, Da Costa; and *Helicella caperata*, Montagu; but the larva has shown the same readiness to attack any other species that I have hitherto tried, including:—

Helicella cantiana, Montagu; *Hygromia rufescens*, Pennant; *Vitrea cellaria*, Müller; *Helix nemoralis*, Linné; and even the largest examples of *Helix aspersa*, Müller; passing indifferently from one to another in the course of its growth.

When a snail is found, the larva raises itself at once on to the shell and examines it carefully, assuring itself of the presence of its occupant. If unsuited to the size of the larva, the snail is left and the search resumed. If it is satisfactory, the larva (more especially in its earlier stages at least) then proceeds to sound the surroundings, reaching out to its full length and ranging about on all sides above and below, but retaining all the while its hold on the shell by means of the anal clasping-organ. This is done with a view to secreting the snail before attacking it. If the position is found to afford sufficient cover, the snail is soon pushed or dragged into it, till out of sight; otherwise, if it is too much exposed (as on a roadway, for example), the larva endeavours to remove it to a better one. This removal of the snail to a place of hiding may prove a difficult matter, and remarkable perseverance is often shown in the endeavour to accomplish it. The larva takes a firm anal grip on the outer surface of the shell, and bending over the side, plants its head on the ground beneath; then, taking hold of the ground with its mandibles, it proceeds to "punt" the snail backwards over the ground, so far as possible in a straight line. Where an obstruction occurs, in the endeavour to pass it, the larva will often raise the snail entirely into the air and throw it forward bodily, but never losing its hold upon the shell. If in the meantime the snail appears and attempts to crawl away it is attacked with the mandibles and driven back. From time to time the larva returns to the summit of the shell to try the surroundings as before, afterwards going back to its task, which, if no cover should be found, may often be continued for an hour, or, as I have once noticed, for as much as three hours before the snail is attacked. It is advisable, when feeding the larva, to provide some loosely placed moss, into which it will soon carry the snail out of sight. In the case of larger larvæ (about 14 mm. and over) the snail is generally attacked very soon, without any attempt to remove it, however exposed the position may be. Larger snails (and I refer especially to *H. cantiana*) seem instinctively to

know their danger when this horrible parasite has attached itself to their shells, and will do their utmost to dislodge it by making rapid contortions of their shells around them as they crawl, even to the extent of overbalancing themselves, and while the larva perhaps lies motionless on the shell. It is surprising that at such times the larva retains its hold or escapes injury, but it quickly takes up a position near the orifice and makes a ferocious onslaught with its mandibles, which probably soon overpowers its wretched victim; I have, however, more than once seen a large *H. cantiana* throw off its assailant and escape.

When the larva enters the shell it lies inside, against the outer wall, and gradually absorbs the moisture, finally consuming the whole or the greater part of the body of the mollusc. After a period varying from eight to sixteen days the shell is thoroughly cleaned out, preparatory to a succeeding period of inactivity and moulting. The larva may then be heard scraping with its mandibles within the shell, and may be seen making a number of journeys backwards, from the centre of the spire to the orifice, to eject from the shell the accumulated and unconsumed matter. The hairy processes seem to aid the work, as a brush, while the larva shuffles backwards down the shell. As the terminal segment reaches the orifice, the anal clasper grips hold of the edge, and, by an undulating movement of the body, the slimy matter is ejected from the shell. I once found a very large larva thus engaged at 10.30 p.m. (having already been working for perhaps half-an-hour). I then watched it for an hour and a half, while it made nine journeys down to the orifice, mostly at intervals of three to five minutes, and with generally about twenty to twenty-five of these undulating movements at the end of a journey. After this I ceased observing it, but I have found that with varying intervals the work may extend over the greater part of a day. In this way the interior of the shell is at length thoroughly cleaned out and made fit for habitation. The larva, which has become gorged with food almost beyond recognition (the dark scuta appearing as isolated patches on the distended white body), then thrusts itself up, with its head towards the centre of the spire, and prepares for moulting, which takes place about four or five weeks from the time of entering the shell, the skin being then cast towards the orifice, where it sometimes closely stops up

the entrance. While the summer lasts, the undeveloped larva, as a rule, evacuates the shell about forty days after entering it, and goes off in search of another. Excluding the shorter feeding interval (July to September) in the year of hatching, it may thus devour as many as three, or perhaps four snails in the course of the summer, moulting once in each case before leaving the shell. But it often ceases feeding as early as July, and in one example, at least, under notice this year, the first shell entered by the larva on June 2nd, after hibernation, was not left afterwards. In such cases the larva, on moulting, reassumes the winter form (which is referred to below), and the growth is again suspended until the following year. From examples under observation, this early return to the winter form seems to be caused by a period of low temperature preceding the time of moulting. An instance of it occurs in the following incomplete record of a remarkable larva:

1900, July 8th: Larva (length about 8 mm.) entered *H. virgata* (greatest diameter 8 mm.);

1901, May 30th: evacuated this shell (length about 10 mm.), and entered *H. aspersa* (greatest diameter 8 mm.);

„ July 10th: left this shell (length about 13 mm.), and entered *H. aspersa* (greatest diameter 28 mm.);

„ August 18th: left this shell (length 21 mm.), and entered *H. aspersa* (greatest diameter 25 mm.);

„ „ 31st: seen to be cleaning out this shell (length, at the time, fully 30 mm.).

Unfortunately, in the spring of 1902, it died while still in the winter stage. The larva was doubtless hatched in July 1899, and must therefore have become full-fed in the third year, as seems to be more often the case.

The winter form, into which the undeveloped larva changes about the middle of September, or often earlier, as stated, is incapable of feeding or of more than a heavy grub-like motion, when disturbed. In general outline it much resembles the ordinary form of the larva, but it rather perhaps deserves the term "false pupa." The scuta are absent, the body being almost entirely soft, of a dingy whitish colour, and, except on the last three or four segments, almost hairless. The head is small, rather soft,

and pale, with the mouth parts rudimentary, and the antennæ very short and much modified. The legs are soft and short, with the claws absent and replaced by a small prominence. The processes on the body are much smaller and less distinct, with only a few fine hairs, until the last three or four segments, where they become longer and rather thickly hairy, but with the hairs shorter than in the larva. The terminal processes are likewise shorter, but with the spines long (Plate II, fig. 2a). This skin is cast about the middle of May, and the larva then reappears from the shell in its ordinary form, continuing its life as before, until it is full-fed, in the second, or, probably in most cases, the third summer.

When full-fed, it changes into a second inactive winter form, which more nearly approaches the pupa, and which, like the other, may be assumed early or late in the year, often as early, at least, as July. Though this is very similar to the previous one, it differs from it especially in the much more stumpy form of the antennæ and of the processes on the last three or four segments; the hairs also on the latter are finer and shorter, and the spines on the terminal pair are very short (Plate II, fig. 3a).

Points of difference in the head and last segment of the two forms are figured in the accompanying drawings beside the corresponding parts in the ordinary form of the larva (Plate II).

The two small apical processes in the antennæ of the larva are retained in both winter forms; but what is the "outer" process in the larva becomes inferior and invisible from above in the first form, and partly inferior while visible on the *inner* side in the second form.

These sluggish winter forms (or "false-pupæ," if they may be so termed) appear to possess a strange tenacity of life. A specimen of the second form, lately kept out for examination, passed a day and a half in a solution one-third alcohol and two-thirds glycerine; then, two days afterwards, an hour in turpentine, followed by a day in alcohol and glycerine. Three days after removal from the latter, it seemed so little the worse that, after washing it in alcohol and in water, I put it into an empty shell, which it entered without difficulty, and it appeared to have its usual amount of vitality when examined a week afterwards. Though in a much lesser degree, the same point is noticeable in the ♀ imago, which will live for two

or three hours in the same preservative solution, or return to its dull existence apparently unaffected by an immersion of an hour and a half in whisky half diluted.

An offensive acrid fluid is emitted from both extremities of the body by the two winter forms of the larva, when disturbed; the active form does not seem to possess this resource, but rolls itself into a ring.

In Mulsant's account of the insect ("Histoire Naturelle des Coléoptères de France; Mollipennes:" pp. 422 ff.), pupation is said to take place fifteen to eighteen days before the imago appears. Prior to this, the position within the shell is reversed, so that the head lies in the direction of the orifice (in which respect this second winter form differs from the earlier one). In a single instance this change of position had already occurred when I examined the shell on October 8th, but ordinarily it appears to be made in the spring. At the time of pupation, the skin is cast far back, near the centre of the spire. The skin of the pupa is soft and unprotected, and merely displays rather distinctly the enclosed form of the imago.

When the final change takes place, about the middle of May, the imago moves forward and occupies the intervening space between the pupa and the larva-skin of the previous year, lying with its head thrust against the anterior part of the latter. There are thus, at this point, four stages of the insect represented in the shell. Here the imago remains for some days before it is able to leave the shell. In three female examples observed in the present year, at least eight days were passed in this way, and the case of a male, referred to below, was similar. The imago appears at the end of May or beginning of June, about the same time as the hibernated larva.

The apterous female (Plate I, fig. 4) is elongate and broader behind, with the abdominal segments sharply explanate under the spiracles, so that the sides have a scalloped appearance. It is of a tawny testaceous colour, marked on each segment, except the last, with a pair of large dark-brown digitate patches more or less regular in shape, and thinly covered, especially above, with fine short rufous hairs. The last segment is terminated by two processes with a small palpiform appendage at the apex of each. The supplement to the antennæ found in the larva and retained in both winter forms, reappears very similarly in the female imago. At the apex of the tenth

joint there is a small inner supplementary joint, terminated by a short seta (which is sometimes scarcely apparent), and a smaller process at the outer margin. The antennæ of the female are normally composed of ten joints (omitting the supplement), but the ninth joint is often imperfectly formed, being sometimes confounded with the preceding one, so as to be scarcely visible, and sometimes entirely absent. This deformity may even appear in different degrees in the two antennæ of the same insect.

Among the imagines that emerged this year I obtained only a single male, and this one happened to occupy one of two shells which I examined on May 18th. It seemed inclined to leave the shell, so I removed it, but it proved to be quite helpless and could only lie on its side, in a curved position, twisting the distended abdomen about like a pupa. I put it on some moss in a shady place, and its condition gradually advanced till, seven days afterwards, it was quite strong. For breeding purposes I had therefore to rely on this male alone, and it paired successively with four females (twice over with one of them) on May 25th, 31st, June 2nd, 4th, and 9th, respectively.

In the spring of the previous year a few eggs had been laid by some infertile females, a week after emerging, on the moss in which they were kept; but this year, under similar conditions, the first female that paired passed six days without laying: there was also reason for believing that the eggs are naturally secreted. I therefore cut a piece of fine turf from the Downs, ten inches by six inches and two inches deep, which I fitted closely into a shallow deal box, and on this the females were afterwards kept near an open window. The following is an account of the movements of these four females which I reserved, and the attempt to breed from them.

The first ♀, as stated, was not put on the turf till six days after pairing, namely on May 31st. From May 31st till June 4th she was up about the surface, generally resting in an exposed position on the short herbage, during each day, but going down every evening under the grass. On June 5th she came up in the morning and rested in the usual attitude on a short blade of grass, with the heavy body curving under her, and thus remained, never leaving the position, so far as I know, day or night, until June 9th, when she fell off and died without having laid.

A second ♀ emerged on May 26th and paired on the

turf on June 2nd, at 11.30 a.m. She continued to move restlessly about the surface till 3.30 p.m., when she dived down a hole between the turf and the side of the box, and did not appear again.

A third emerged on June 2nd and paired on the turf on June 4th, disappearing on the same day.

A fourth emerged and paired on May 31st, but was not put on the turf till five hours afterwards. From this date, this ♀, like the first, was about the surface (generally resting on the herbage) regularly during the daytime, but always going down under the grass in the evening, until June 9th. I then tried the ♂ again, and she paired a second time, disappearing soon afterwards on the same day.

After June 9th none of them appeared again.

Though it is to a great extent the instinct of the ♀ to hide herself, she seems, in fact, after emerging, to choose more often some exposed position on the short herbage, and to remain clinging to this for hours at a time without moving. From the moment of pairing she proceeds at once to make her way down under the grass (the ♂ probably sharing the same instinct), and after separation—*i.e.* after about forty minutes—disappears very shortly, as it seems, into the turf, where she lays her eggs and dies. The failure of the first of these four was perhaps due to the absence of natural conditions in the first week.

On June 20th I examined the turf in search of ova. The body of one ♀ was found resting in a perpendicular position between the turf and the side of the box. The body seemed half empty, but I could find no eggs that had been laid. Probably this was the second ♀ mentioned above.

The bodies of the other two I found in the bottom of the turf (*i.e.* two inches deep), each lying with its contents emptied in a compact heap within a distance of half-an-inch from it. Doubtless both had died very soon after laying.

The egg is nearly spherical, about 1 mm. in diameter, and of a pale yellow colour. Roughly speaking, there were about thirty to thirty-five eggs in each heap.

It was a mistake to disturb them so soon, but the period of development proved to be much longer than I expected, and to leave them as they were, and unobserved, was unsatisfactory. In an endeavour to preserve natural

conditions, the evils of excessive moisture and excessive dryness crept in, and worked serious injury in the first week or ten days. On July 2nd the embryo began to show signs of development, and on July 8th the form of the young larva was discernible. After this they advanced rapidly till the first hatched on July 20th, or about six weeks from the approximate date of laying. But meantime the greater number had fallen off in various stages of development, and only five, out of perhaps sixty-five, survived, hatching respectively on July 20th, 22nd, 24th, 25th, and 26th. One of these was a cripple and another was lost by an accident.

At the time of hatching, with the exception of the conspicuous black ocelli and a few reddish hairs, they were nearly white, the head and the shields about the segments attaining their darker colour several hours afterwards. The length is about $2\frac{1}{2}$ mm.

Of the three that remained, two began to feed about thirty-six hours after hatching; the third clung to its egg-shell for twenty-four hours, and refused food for three and a half days. The snails at length given them were *Helicella caperata*, and *Hygromia rufescens*, 3 to 4 mm. in diameter.

In these three examples (as also the one that was lost) I noticed most of the instincts of the older larva, including the feigning of death for as long as fifteen or twenty minutes at a time. There was no attempt to push the snail away, but a decided tendency to work underneath it, perhaps with the same purpose. More than once a snail that began to appear from the shell was sharply struck with the mandibles and driven back; in another case the hardened film quickly thrown by the snail as a barrier across the orifice was cut away by the larva after an hour and a half's work, and the shell was then entered. The ultimate loss of these larvæ was perhaps largely due to the period of exceptionally cold weather that followed the time of hatching, and particularly so in the Cotswolds, where I happened to be staying. The fragmentary account of them, so far as it goes, may, however, be worth recording.

Larva (*a*) hatched on July 20th, and entered the first shell on July 21st; partly devoured this snail; left it and entered another on August 2nd, but afterwards became entangled inside the shell, and died without having moulted.

Larva (*b*) hatched on July 22nd, and on July 25th entered the first shell, in which it became entangled, and died without moulting.

Larva (*e*) hatched on July 25th, entered the first shell on July 26th, and, after partly devouring the occupant, left it and attacked a second on July 28th; was ejected some hours afterwards by the latter, and left entangled; I released it and put it back on the first shell, which it at once re-entered, but it afterwards died without having moulted.

I have nevertheless found the exuviæ of the young larva at about 3 mm. in very small snail-shells (3–4 mm. in diameter), and it seems more probable that the economy of the larva in its infancy is the same as in its later growth, and that under ordinary circumstances the first shell is not left till after moulting, in the usual manner. It would thus be able to attain a length of about 4 mm. at the time of entering the second shell, at which point it is to be found feeding, about the middle of September, prior to hibernation. After this, the growth of the larva is regulated by the size of the snails it happens to meet with, its length being increased, as I have found in most cases observed, roughly by about half the greatest diameter of the snail attacked. The female imago may thus be no more than 8 mm. in length, or, on the other hand, probably not far short of 30 mm. On the Downs, larger snails such as *H. cantiana* are seldom met with by the larva, and the average length of nine naturally-reared females which emerged this year was 10·7 mm. only.

In regard to the life history of the male, Mulsant mentions the fact that out of one hundred and fifty shells containing larvæ, Desmarest obtained only two males, while M. Rouget obtained only one male among about two hundred females. Appended are a few details bearing on this point.

As already mentioned, all of five larvæ which I reared in 1900 were females.

The shells collected in the autumn of 1901 and early in 1902 varied from 4 to 12 mm. in their greatest diameter (*i.e.* the measurement across the shell to the outermost point of the orifice). Of those larvæ that were full-fed, nine were females and five were males. All of the females emerged, but four of the males died as pupæ (the fifth was taken in February; the others in September).

Another shell contained the remains of a male pupa which had probably failed to emerge in the previous spring.

The shells containing these six males were :—

Two of them *Helicella virgata*, Da Costa; 8 and 9 mm. in diameter respectively.

Four of them *Helicella caperata*, Montagu, 7, 7, 7, and 8 mm. in diameter respectively.

Another shell found at the same time, containing a male pupa skin, was that of *Helicella caperata*, 6 mm. in diameter.

The following table shows the greatest diameter of thirty-seven winter shells (all naturally occupied by larvæ), and the state of the insect after hibernation :—

2	shells of	4	mm.	in	diam.	produced	2	undeveloped	larvæ.	
2	,,	5	,,	,,	,,	2	,,	,,		
5	,,	6	,,	,,	,,	4	,,	,,	and 1	♂.
6	,,	7	,,	,,	,,	3	,,	,,	,, 3	♂.
6	,,	8	,,	,,	,,	4	,,	,,	,, 2	♂.
5	,,	9	,,	,,	,,	4	,,	,,	,, 1	♂.
11	,,	10–12	,,	,,	,,	2	,,	,,	,, 9	♀.

In other words, all full-fed larvæ occupying shells of 6–9 mm., and averaging $7\frac{1}{2}$ mm., were males, and all those occupying shells over 9 mm. were females; which result might, in fact, be expected approximately, considering that the male imago never perhaps attains the minimum length of the female.

The females probably outnumber the males very considerably, while the male larva must be sought for in shells of a small size only. But, apart from these considerations, the male seems, for some reason, to be more difficult to rear than the female—possibly owing to the fact that it is more likely to complete its limited growth early in the year, and so to be subject to a longer period of exposure to the exigencies of weather.

The number of eggs laid by the female may be as many as three hundred, or even more; but the female, which is little more than an egg-magazine, varies in size to an extraordinary degree, and the number of eggs must vary greatly in proportion. In a female of 19 mm. I found two hundred and sixty-seven, but in smaller examples the numbers were far short of this. The two that laid (presumably 10 mm. and 13 mm. respectively) cannot either of them have laid more than about forty; the abdo-

men of another (11 mm.), nine days after leaving the shell, contained thirty-three; while in another (8 mm.), seven days after leaving the shell, there were only four or five developed ova, and the abdomen *could* hardly have contained more than fifteen or twenty.

The following case of cannibalism occurred in the present year:—

Two larvæ, "A" and "B," were due to leave their shells about the same date, early in July, and both had already moulted. "A" left its shell first, and escaping unobserved into the division of "B," entered the shell and attacked and devoured the unfortunate occupant. The unconsumed remains of "B" were afterwards cast back and left near the orifice of the shell, and the larva "A" in due time moulted, evacuating the shell thirty-five days after the probable date of entering it.

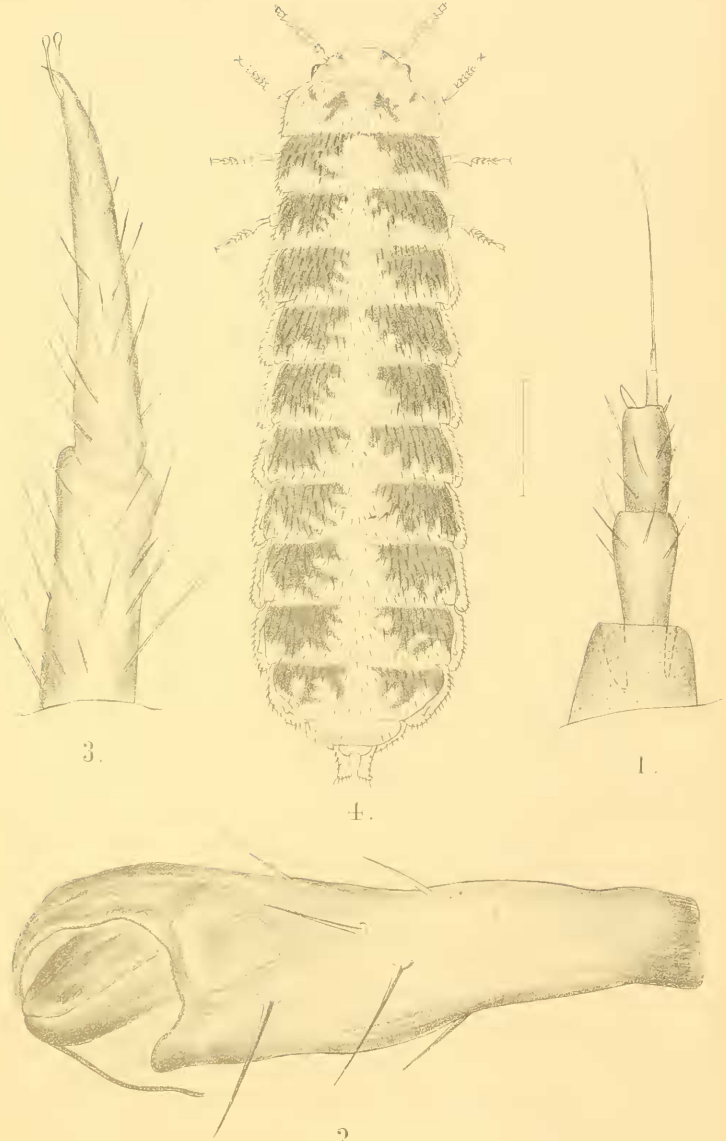
Among a number of shells examined, which have contained larvæ, I have not noticed any clear case of parasitic attack on the species. I am indebted to Mr. C. O. Waterhouse for his kind assistance in connection with the subject of this paper.

Explanation of Plate I.

Figure 1. Left antenna of larva, partially withdrawn.
„ 2. Spiracle of larva, projecting from horny encasement.
„ 3. Part of intermediate leg of larva.
„ 4. Female imago.

Explanation of Plate II.

Figure 1. Active form of larva; part of head, showing antennæ and mandibles (antennæ extended).
„ 2. Winter form of undeveloped larva; part of head, showing antennæ and mandibles.
„ 3. Winter form of full-fed larva; part of head, showing antennæ and mandibles.
„ 1a. Active form of larva; last segment.
„ 2a. Winter form of undeveloped larva; last segment.
„ 3a. „ „ „ full-fed larva; last segment.



3.

4.

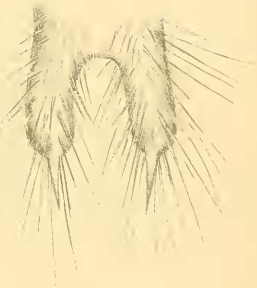
1.

2.

L.R Crawshay del. Mintern Bros. lith.

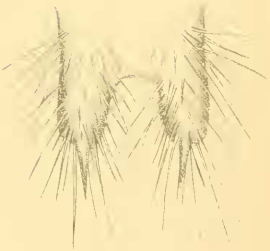
Transformations of Drilus flavescens.

1.



1a.

2.



2a.

3.

3a.

L. R. Crawshay del.

Mintern Bros. lith.

Transformations of Drilus flavescens.